

CHAPTER 1

Functional Trait Approaches for the Study of Metazooplankton Ecology

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1.1 A Brief History of Trait-based Approaches and their Application to Aquatic Ecology

Functional trait-based approaches have increased in popularity in ecology since the turn of the millennium. There are a number of advantages to such approaches that explain their widespread adoption. In particular, examining traits present in a community can increase the mechanistic understanding of how environmental factors may influence its structure and how community shifts may in turn influence ecosystem processes (functioning). Moreover, utilizing lists of observed traits across individuals, rather than lists of species present within communities, enables a comparison across regions that may have very different taxonomic composition, while expressed traits that are behavioural, physiological or morphological can sometimes be directly compared as these are common to all life forms. Particularly applicable to plankton communities, the use of functional traits can even enable comparison of marine with freshwater environments, broadening our understanding and predictions of the ecological roles of aquatic organisms (Hébert et al. 2016a). Together, the traits expressed in a community can thus provide an indication of organismal strategies and roles as well as the niche space occupied that can then be compared across habitats and ecosystems (Litchman et al. 2013).

More recent practice describes organisms as a continuous distribution of traits along environmental gradients (Kenitz et al. 2018), a concept forming the core of the emergent field of functional biogeography (Violle et al. 2014). Such an approach can allow for a greater exploration of trait patterns and trade-off relationships (Kjørboe 2011), which can prove useful in predicting novel trait

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assemblages or organismal strategies under different conditions (Chen et al. 2018). In a broader context, investigating trait (spatial) distributions and (temporal) successions can provide mechanistic insight into how organisms may respond to environmental drivers and changes, which can in turn be implemented into scenarios of future global change (e.g., warming responses; Burrows et al. 2019). Using traits rather than taxonomic affiliation also enables the assessment of functional diversity, which can depict more clearly the degree to which organismal roles in ecosystems are complementary or redundant (Hooper et al. 2005).

In aquatic environments, the use of functional traits has been adopted for a variety of organisms, including both marine and freshwater plankton, fish, benthic macroinvertebrates, and macrophytes. Amongst the plankton, functional approaches—generally perceived as the precursor to functional groups—began to be used earlier for phytoplankton, in large part because of the ground-breaking work of Ramón Margalef (1960–70s) and Colin Reynolds (1980–90s) relating “life forms” or “functional morphologies” to environmental conditions (Weithoff and Beisner 2019). As such, phytoplankton ecology is more readily translatable from the pioneering work done earlier in the trait-based ecology of terrestrial plant communities; e.g., Tilman et al. (1997), Walker et al. (1999), Reynolds et al. (2002), Weithoff (2003). Amongst metazoan animal communities, however, functional traits were applied relatively early to aquatic organisms. This is especially the case for stream benthic invertebrates largely because of the well-developed functional groups based on food web position and feeding strategies outlined in the river continuum concept (Cummins and Klug 1979, Vannote et al. 1980). One particularly applied aspect that has emerged from the trait framework in stream benthic ecology is the widely adopted development of bioindicators for habitat quality based on macroinvertebrate tolerance to stress. The early use of benthic macroinvertebrate traits to derive bioindicators likely occurred because this group of organisms is relatively long-lived (integrating information from a few seasons), not particularly motile (reflecting local habitat conditions), and exhibits highly variable response and tolerance to stress (Wallace and Webster 1996), unlike many other aquatic organisms. Fish ecologists were also relatively early adopters of trait-based approaches, mainly focusing on morphological size indicators that influence feeding, swimming and agility (Lankford et al. 2001), with more recent inclusion of metabolic traits to infer the contribution of fish communities to ecosystem processes (Barneche et al. 2014). Much of the earliest uses of traits for aquatic organisms were in relation to the physical-chemical constraints present in aquatic environments; e.g., phytoplankton movement and morphology in relation to lake stratification/mixing (Reynolds 1984), or fish and benthic invertebrate feeding and morphologies in relation to streamflow and dissolved oxygen (Poff et al. 2006, Keck et al. 2014). It is possible that the less obvious effect of lake and ocean physical mixing on the relatively motile zooplankton may have led to a delayed interest in trait-based approaches for this group of organisms. However, the use of chemical elements to characterize organisms at different levels of organization that emerged three decades ago in the form of “biological stoichiometry” can be considered amongst the earliest applications of traits to characterize zooplankton, especially with respect to linking particular taxonomic groups to ecosystem processes (e.g., nutrient recycling; Elser et al. 2000).

Amongst the various organisms that can be classified as metazooplankton, it is for the crustacean component that trait-based approaches have been most commonly used, as this group is globally distributed, very abundant, and a large proportion of zooplankton diversity is known. A first compilation of potential crustacean zooplankton functional traits was done by Barnett et al. (2007) for freshwater species of eastern North America. Since then, Litchman et al. (2013) have further developed a more general conceptual framework within which to consider zooplankton traits, similar to the one previously developed for phytoplankton (Litchman and Klausmeier 2008). Subsequently, Hébert et al. (2016a, b) expanded the original trait compilation of Barnett et al. (2007), including a broader range of crustacean traits more specifically related to ecosystem function in both freshwater and marine environments. Additional trait syntheses for marine species include the databases developed by Benedetti et al. (2015; copepods), Pomerleau et al. (2015; copepods, amphipods, euphausiids,

pteropods, ostracods, hydrozoans), and Brun et al. (2016; copepods). Perhaps one of the reasons why there are more trait data compilations for marine species is that there exists more accessible resources documenting species-specific (mostly morphological) information for a wide taxonomic coverage, including Mauchline (1980, 1998) that contains valuable data on the biology of marine calanoids, mysids and euphausiids, or periodically-updated online platforms, such as Razouls et al. (2005–2019) and the World Register of Marine Species (2000–2019). As with phytoplankton (Bruggemann 2011), metazooplankton traits may be phylogenetically constrained to some degree, given that phylogenies were based upon morphological similarities/dissimilarities. The trait synthesis work to date has demonstrated that there are only a few traits for which we have large taxonomic coverage to enable broad application to metazooplankton communities, with trait data being disproportionately more reported for crustaceans relative to other metazooplankton representatives. In particular, quantitative traits that relate to ecosystem processes are more sparse, especially in freshwater ecosystems (Hébert et al. 2017). In this chapter, we will focus on knowledge related to metazooplankton traits, thus not including planktonic phagotrophic protists such as ciliates (see Santoferrara and McManus 2021, this book, Chapter 5), foraminiferans or radiolarians (see Boltovskoy and Correa 2021, this book, Chapter 6).

1.2 Most Commonly used Traits in Metazooplankton

As in other subfields of ecology, functional traits and their relation to community and ecosystem processes have become an active area of research for metazooplankton ecology. Traits are defined as individual-level measurements of behavioural, morphological, molecular, phenological or physiological characters that can influence fitness, while encapsulating information on population, community and ecosystem processes (Table 1.1; Violle et al. 2007). The trait framework can be organized into two main types, dependent on whether organismal traits are examined through the lens of (i) factors determining community structure and assembly processes or (ii) the direct influence of traits on ecosystem processes (Lavorel and Garnier 2002). In the former category, traits are often referred to as “response traits” while in the latter they can be considered as “effect traits”. It should be noted, however, that it is the way in which traits are used to address ecological questions that often determines whether they are considered response or effect traits. Some traits are more versatile than others, directly affecting processes at multiple scales and thus falling into more than one trait category (Table 1.1). For example, morphology such as distances between setae that determine the size of phytoplankton prey captured by filter feeding crustacean zooplankton could be considered as a response trait to the feeding preferences of competing zooplankton and to the phytoplankton community present in a habitat, or it could be considered an effect trait influencing

Table 1.1: Integrative framework linking traits to levels of organization and ecological parameters of interest. Some traits may be related to specific ecological parameters and thus operate at particular levels of organization (“mono-type” trait); e.g., response traits such as temperature optima or stress tolerance dictating community composition and succession along environmental gradients. Other, more versatile traits may encapsulate information regarding several or all levels of organization (e.g., body size, growth; *). Adapted from Hébert et al. (2017).

<i>Level of organization and application</i>	<i>Ecological parameters of interest</i>	<i>Commonly used trait type</i>	<i>Examples of traits for metazooplankton</i>
Ecosystem	Ecosystem functioning (properties and processes)	Effect traits	Body size*, growth*, respiration, excretion, clearance rates
Community	Community structure and assembly processes	Response	Body size*, growth*, temperature optima, stress tolerance (e.g., starvation, hypoxia)
Population	Population dynamics	Demographic	Body size*, growth*, generation time, dispersal
Individual	Individual fitness and performance	Life-history	Body size*, growth*, fecundity, individual performance- or survival-related traits

phytoplankton community composition, overall biomass pools or primary productivity. Conversely, there are several “mono-type” traits, i.e., those that can only or primarily be regarded as either a response or effect trait (Table 1.1; Violle et al. 2007). Although some traits may indirectly affect different ecological parameters across levels of organization, “mono-type” traits are typically those that exert direct effects at only one level of organization (Table 1.1; Hébert et al. 2017). For example, amongst the plankton, thermal growth optima would mainly be perceived as a response trait (i.e., dictating community assemblages along temperature gradients; Burrows et al. 2019), while carbon (C) export efficiency is essentially considered as an effect trait (Litchman et al. 2015).

Functional traits can be either qualitative or quantitative in nature, both types being useful in estimates of functional diversity (Section 1.6). Estimating functional diversity indices permits comparison across communities, with most indices allowing for the incorporation of both qualitative and quantitative traits via the use of Gower distances (Petchey and Gaston 2002, 2006, Villéger et al. 2008, Laliberté and Legendre 2010). Several quantitative traits can be considered as “hard” traits (i.e., informative though hard to measure traits) that are often estimated more broadly via “soft” proxy traits (i.e., more readily-measurable correlates of hard traits) that may or may not be quantitative (Hodgson et al. 1999); e.g., several physiological traits are mass-dependent, and their values can sometimes be inferred from body size. For a non-exhaustive list of soft and hard trait associations in zooplankton, see Table 1 in Hébert et al. (2017).

To conceptually represent relations among traits, Litchman et al. (2013) and Hébert et al. (2017) provide frameworks within which the functional traits of metazooplankton can be classified. The Litchman et al. (2013) framework focuses on ecological functions of traits related to metazooplankton feeding, growth/reproduction and survival/mortality. The framework proposed by Hébert et al. (2017) emphasizes inter-related traits based on organismal bioenergetics (energy budget) and considers more specifically potential associations between organismal and ecosystem functions. We combine these perspectives to summarize the general state of knowledge to date for metazooplankton traits, relating them to their primary organismal function, sometimes listing more than one primary function (organismal functions are indicated in capitals in the following outline). Within this framework, qualitative and quantitative traits are classified according to whether they relate primarily to morphology, behaviour, physiology or life history. For most traits, we provide a brief description of how they can be measured and examples of how they can be used as either response or effect traits.

1.2.1 Morphological Traits

Body Size (SURVIVAL/MORTALITY, GROWTH/REPRODUCTION, FEEDING)

Expressed in length or mass, body size is one of the most widely used traits for all groups of metazooplankton. Although most precise if measured at the individual level, taxon-specific means of body size from particular habitats are commonly employed. Body size can act as a proxy for many traits via well-established allometric relationships, especially in poikilothermic organisms for which various biological rates can be reasonably well estimated from body size and ambient temperature (Hébert et al. 2016a). Body size is often considered a “master trait”, as it is one of the main soft traits for metazooplankton, providing a value that summarizes many other, harder to measure traits (see Section 1.4), such as physiological traits (e.g., clearance, excretion, growth, respiration; Hébert et al. 2017) or behavioural traits (e.g., body-size dependence of occupied depths in the water column or in diel vertical migration patterns; Ohman and Romagnan 2016).

As a master trait, body size can be used both as a response and effect trait, as it equally integrates environment-induced organismal responses (e.g., to temperature or predation; Patoine et al. 2002, Daufresne et al. 2009) and the influence that organisms can exert on ecosystem processes (e.g., the contribution of community-weighted mass-dependant physiological rates to elemental flow; Hébert

et al. 2017). In a multi-trophic context, integrating body size information can provide insight as to how the size structure of food webs may vary along environmental gradients (Kenitz et al. 2018).

Volume to Biomass Ratio (SURVIVAL/MORTALITY, GROWTH/REPRODUCTION, FEEDING)

This trait is one that separates crustacean zooplankton (cladocerans, copepods, mysids, euphausiids) from the rotatorian (rotifers) and gelatinous zooplankton (salps, ctenophores, cnidarians, pteropods, semi-gelatinous chaetognaths) based on body C-density (Litchman et al. 2013). Gelatinous zooplankton tend to have very large volumes relative to mass density compared to crustaceans, resulting in the former having larger body sizes that can increase prey capture rates and reduce their own exposure to predation.

Defence (SURVIVAL/MORTALITY)

Freshwater cladocerans are the crustacean zooplankton with the best-known inducible defence system. For example, many *Daphnia* species are able to develop elongated “helmeted” forms when predators are present. This is an especially effective method to evade gape-limited invertebrate predation. Another example of polymorphism for inducible defense is the ability of some rotifers such as *Brachionus* to develop lateral spines in the presence of predator kairomones; however, given that this is energy-demanding, the expression of such defence structures may not be possible under competition pressure, as observed in *B. calyciflorus* (Yoshida et al. 2003). The high sensitivity and plasticity of such defence-related features makes them good response traits to detect predation signals.

The development of sensory systems is a key adaptation to help zooplankton evade predation. Antipredator sensory modalities include the ability to detect light (photoreception), chemicals (chemoreception) and fluid motion (mechanoreception; Buskey et al. 2002, 2011). Upon the detection of a threat, a response is triggered (e.g., escape behaviour or migration; see sections on Motility and Migration). The development of some neurophysiological features can influence the efficiency of such antipredator systems. For example, in copepods, mechanoreception is used to detect hydrodynamic disturbances created by the motion of predators; once a threat is perceived, copepods must in turn react rapidly, and this response can be faster in species having developed myelinated nerves (Buskey et al. 2002, 2011). The discrepancy in response latencies between myelinate and amyelinate copepod species can have a significant effect on predator avoidance efficiency (and thus survival), with differences in response latencies being greatest across larger copepod species given that nerve signals must be conducted over relatively longer distances (Buskey et al. 2011). In this context, the presence of myelinated nerves, or other analogous neurophysiological features, could be considered as a defense-related trait.

Bioluminescence, primarily present and studied in marine zooplankton, has been considered a warning signal towards predators, aiding in the survival of some taxa of chaetognaths (Thuesen et al. 2010) and gelatinous ctenophores and planktonic cnidaria (Haddock and Case 1999). Bioluminescence may also confer crypsis at depth where there is little ambient light, preventing detection by predators (counterillumination), in some gelatinous zooplankton as well as in euphausiids (Herring 1999, Johnsen 2005). However, there is variation in functional purposes of bioluminescence, and it may also serve in some cases for reproductive purposes (Herring 1999).

Given that most planktonic animals are solitary across all aquatic environments, it is hard to include coloniality as a trait on its own, as has been done for phytoplankton. At least one group of free-swimming rotifers (Conochilidae) has a colonial life-form, which likely helps protect them from predation by gape-limited vertebrate and especially invertebrate predators (Gilbert 1980, Diéguez

and Balseiro 1998). Coloniality is relatively more observed in gelatinous zooplankton, such as siphonophores, salps or pyrosomes (Mackie 1986). Defensive reactions can be highly developed in such colonies, but often in the form of escape responses through jet propulsion. For siphonophores and salps, coloniality enables coordinated locomotion, enhancing the control and efficiency of swimming movements (Mackie 1986, Madin 1990). For example, physonect siphonophores use multiple clonal individuals (“nectophores”) to propel aggregate colonies, with nectophores from the base of the colony affecting the direction and magnitude of whole-colony movements differently from nectophores situated in the colony apex (Costello et al. 2015).

Transparency (SURVIVAL/MORTALITY)

The degree to which metazooplankton are transparent and therefore less prone to detection by visual predators can also vary across taxa. Gelatinous and rotatorian taxa, with their high volume to biomass ratios and high-water content, may be more transparent (Litchman et al. 2013). On the other hand, normally transparent or translucent crustacean zooplankton may be more pigmented owing to lipid deposition if they are exposed to colder waters, such as those experienced at deeper depths or in winter months (Ohman et al. 1998, Grosbois and Rautio 2018). In the absence of predation threat, crustaceans can also retain protective pigments when exposed to high levels of UV radiation (Hylander et al. 2009). Thus, seasonal variation in this trait is possible. In marine environments, gelatinous zooplankton like salps and pteropods are almost exclusively transparent, while ctenophores show a wide variety of colouration, ranging from almost completely transparent to strongly pigmented.

Food Particle Size and Feeding Apparati (FEEDING)

Food particle size can be expressed as quantitative ranges or bracketed size categories (Barnett et al. 2007). Preferred or selected food size range or category can be defined based on laboratory analyses or *in situ* incubation experiments of single taxa with a range of prey sizes. Mesh size or setulae distance mechanistically extends the prey size range trait but applies only to zooplankton species that filter feed using setulae. The distance between setulae will define the prey size most frequently captured and can thus be considered a trait of that organism or taxon. Other zooplankton may be limited by gape size (e.g., rotifers, chaetognaths) or relatively unlimited such as in the case of cnidarians.

The presence, morphology or composition of particular features associated with feeding apparati can also be indicative of preferred diet. For example, copepods use the gnathobases of their mandibles to grab and crush their prey, and in some species gnathobases can exhibit diet-specific characteristics, such as silica-based tooth-like structures that facilitate the breaking of silicified diatom frustules while protecting the copepod from mechanical damage (Michels et al. 2012, Michels and Gorb 2015). Analogously, in rotifers, certain features of their feeding apparati can reflect diet type or trophic group. For instance, the mastax (i.e., pharynx-like apparatus enabling mastication) can contain calcified jaw-like structures (termed trophi) that highly vary in shape: trophi can take the shape of grinding ridges in suspension feeders, whereas they can be forceps-shaped in carnivorous species, which enhances their grip on prey; in ectoparasitic rotifers, the mastax can serve to grip onto hosts (Barnes 1980).

Together with body size and food web position, morphological traits informing on diet type or food size range can prove useful to determine “who eats whom” in food web models requiring an *a priori* establishment of possible interactions. Taxon-specific information for food particle size in freshwater crustacean zooplankton has been compiled by Barnett et al. (2007). As for using this trait in a response–effect trait framework, it can be used both ways: food size can be mediated by intraguild competition or resource availability within habitats (response trait), but can also be indicative of zooplankton top-down control on phytoplankton standing stocks or community composition (effect trait).

1.2.2 Behavioural Traits

Feeding Mode (FEEDING)

Crustacean zooplankton differ in their foraging tactics, based on swimming behaviour and feeding via passive or raptorial approaches (DeMott and Watson 1991). Cyclopoid copepods are generally raptorial, most often actively capturing motile prey detected via mechanoreception. On the other hand, Calanoid copepods are usually classified as stationary suspension feeders, but in rare cases as current cruisers (e.g., *Epischura lacustris*; DeMott and Watson 1991). Stationary suspension feeders can detect prey at a distance and re-orient their body position or change feeding currents to increase capture rates (Strickler 1982). Current cruisers move continuously while producing a feeding current to passively capture prey.

Most cladocerans exhibit filter feeding, although predatory freshwater species (e.g., *Polyphemus*, *Bythotrephes*, and *Leptodora* spp.) are raptorial. However, predatory mysids, often present in deep glacial relict lakes, are filter feeders. Freshwater cladoceran filter feeders can be further classified into the *Daphnia* (D)-type, the *Sida* (S)-type and the *Bosmina* (B)-type depending on the degree to which feeding positions are stationary (D and S-types) versus involving active swimming (B-type) (DeMott and Kerfoot 1982). B-type feeders thus resemble copepod current cruisers. D and S-types draw water with particles through their carapace openings, separating particles using thoracic appendages possessing fine filter plates (on different legs to separate the D and S-types) that collect food particles from the feeding current, and drawing them into the food groove. To this, Barnett et al. (2007) have added *Chydorus* (C)-types to represent zooplankton that feed by scraping periphyton from surfaces. As with other feeding-related traits, diversity in feeding modes can reflect environmental constraints (response traits) while informing on the top-down control exerted by zooplankton (effect traits), with some feeding modes being associated with greater feeding rates (stronger influence on resource biomass) or selectivity/specificity (stronger influence on resource community composition).

In part because of the larger diversity of life forms, marine zooplankton show a wide array of prey capture techniques including using tentacles as webs by sit-and-wait predators, ambush predation, filter feeding or prey baiting through hanging sticky droplets on a thread (all techniques used by ctenophores; Haddock 2007). While filter feeding is most commonly observed (cnidarians, ctenophores, euphausiids and salps), raptorial predation through forward darting to capture prey may also be present (e.g., chaetognaths; Hinde 1998). Although more specific, mucous-mesh grazing is also a common feeding mode (pelagic tunicates and pteropods) that implies the capture, consumption and re-packing of very small particles. Erroneously perceived as non-selective filter feeding in the past, the use of adhesive mucous mesh can be prey-specific, with important functional variations in filter mechanisms and hydrodynamics across taxa (Conley et al. 2018).

Food Web Position (FEEDING)

The degree to which zooplankton are herbivorous, carnivorous or omnivorous can also vary. Barnett et al. (2007) classified this trait into 5 categories: pure herbivores, omnivores that are primary herbivorous, omnivores, omnivores that are primarily carnivorous and pure carnivores. This trait is a good example of how trait-based classification may be a means to simplify diversity across groups of zooplankton, where purely carnivorous zooplankton can include representatives of various taxa from marine and freshwater habitats; e.g., ctenophores, cnidarians, amphipods and predatory cyclopoids and cladocerans.

Defining trophic groups can be based on gut content analysis, and in more recent decades on trophic tracers involving stable isotopes (of C and N, most commonly), trace elements, fatty acids, and bulk tissue- or compound-specific stable isotopes (Pethybridge et al. 2018). While most techniques align well when applied to simple diet mixtures, they often tend to diverge with diet complexity

(Nielsen et al. 2017). Biochemical tracers have various advantages (e.g., high specificity, low sample size required) but they can be assimilated over relatively long time scales, providing trophic information that may differ from gut content analyses, for instance. As a result, there is now an increasing number of studies employing complementary approaches to reduce biases of single methods (Schmidt et al. 2006). Through the use of such techniques, trophic groups (based on diet composition, niche width or trophic position) can be characterized for individuals from different environments, and general taxonomic tendencies can be identified. Trophic classification can be applied most easily to adult stages, as ontogenetic niche shifts in feeding preferences by zooplankton may occur in some groups. It should be noted that some taxa may show parasitic feeding (e.g., some cnidaria and at least one ctenophore and many copepod species; Kabata 1982, Haddock 2007, Jiménez-Guri et al. 2007); parasitic feeding could be used as a trait, although many parasitic organisms are not technically free-living and whether they are included will depend on the extent of the community being considered.

As highlighted in the “Food Particle Size and Feeding Apparati” description, food web position is a valuable information to consider to analyze multi-trophic interactions with more realism (Gsell et al. 2016, Kenitz et al. 2018). An appreciable amount of information on food web positions occupied by crustacean zooplankton in both marine and freshwater environments can be found in Hébert et al. (2016b).

Motility (FEEDING, SURVIVAL/MORTALITY)

Metazooplankton differ in their motility traits with some having greater swimming speeds than others based on different movement types. Motility expressed by metazooplankton taxa has much to do with the way in which they capture prey. Thus, raptorial predators such as copepods may demonstrate extremely rapid movements following periods of relative stasis while cruising feeders may show low but consistent velocities. Salps are barrel-shaped planktonic tunicates that move via jet propulsion created when they contract to pump water through their bodies (see coloniality in the section on Defense), from which they also retain phytoplankton food by filter feeding. Zooplankton motility can also reflect predation to which individuals are exposed through their escape response. For example, some rotifers such as *Polyarthra* can swim slowly when feeding, and then can make large jumps (of several times body length) using their “feather-like” appendices when a predator is detected (Gilbert 1985). Similarly, some ctenophores swim through undulating movements, while others appear to have “darting” motions.

Metazooplankton motility traits can be characterized based on the various types of movement mechanisms: swimming using appendages (copepods and cladocerans), rowing (some cnidaria), undulation (ctenophores, some cnidaria) or jet propulsion (salps and some cnidaria). Given the tight link between motility and feeding traits (active/motile versus passive/non-motile feeders), these are often used in conjunction to determine optimal strategies in different physicochemical environments. Along with size-based food preferences, this trait combination can predict predator-prey interactions (e.g., Kenitz et al. 2018).

Migration (SURVIVAL/MORTALITY, GROWTH/REPRODUCTION, FEEDING)

Diel vertical migration (DVM), or diel horizontal migration in shallow freshwater ecosystems (DHM), are ways in which zooplankton can evade predation, but usually at a cost to (diurnal) feeding, especially for herbivorous zooplankton (Burks et al. 2002, Lampert 2005, Williamson et al. 2011, Pierson et al. 2013). Many zooplankton will remain in darker, deeper waters or in refugia provided by macrophytes during daylight hours to avoid predation by visual predators such as fish. At night, they migrate to the upper layer where phytoplankton are more abundant, and also because warmer temperatures from the surface are beneficial for zooplankton egg development. Migration-related traits influence immediate survival but also growth and reproduction via indirect effects on their feeding and egg development.

Euphausiids can show extremely large daily migrations in marine environment. In lakes, it has been shown that the tendency to display DVM may vary between populations and can represent an adaptive response to previous exposure to predators (Pangle and Peacor 2006). DVM is thus a response trait that can indicate current or previous predation pressure. However, active transport through daily migration can also mediate C and nutrient vertical fluxes through differential feeding, respiration, excretion and egestion along depths, especially in marine environments where DVM can sustain mesopelagic food webs (Kelly et al. 2019); hence, migration can also be used as an effect trait.

1.2.3 Stoichiometric and Physiological Traits

Feeding Rate (FEEDING)

Clearance or grazing rates can be considered as a trait that reflects grazing or feeding rates. Clearance rates are estimated as the volume of water from which a zooplankton removes prey per unit time (Gauld 1951). Although responsive to environmental conditions (e.g., temperature, food availability), feeding rate estimates is likely to be an important effect trait, influencing phytoplankton productivity and biomass as well as nutrient and energy transfer. Sloppy feeding observed in copepods can also supply a fair amount of dissolved nutrients and C, which can not only support phytoplankton but also heterotrophic bacterial growth and other aspects of the C cycle (Jumars et al. 1989, Steinberg and Landry 2017).

Respiration/Metabolic Rates (SURVIVAL/MORTALITY)

Basal metabolic rate, which maintains body tissues, is likely to vary between metazooplankton, but it has been little studied to date. As a trait, this rate is likely to influence longevity and other metabolic functions such as excretion. Respiration rates can be estimated, usually on an individual level, by measuring changes in oxygen concentration in a small chamber where the individual plankter resides. Alternatively, electron transport system (ETS) activity can also reflect respiration in zooplankton (Bode et al. 2013). At rest, this rate represents the basal metabolic rate, otherwise respiration rate can vary under different conditions and can be affected by behaviour as well. Respiration rates are primarily used as an effect trait, given the direct impact of oxygen consumption and CO₂ release in the environment. The magnitude of this effect, however, depends on the relative proportion of zooplankton biomass in a given system.

Excretion and Egestion (SURVIVAL/MORTALITY, FEEDING)

These physiological functions release dissolved (excretion) and particulate (egestion; faecal pellets) compounds, contributing to N, phosphorus (P) and C cycling. Typically, only N and P under the forms of ammonia and phosphate are measured in zooplankton excretion; only very rarely other organic compounds such as urea or amino acids are measured, despite their potential role in stimulating heterotrophic bacterial activity (Aristegui et al. 2014). For faecal pellets—one of the primary components of the so-called “marine snow” aggregates found in oceans (Turner and Ferrante 1979)—C content is most often quantified as a measure of C export in marine systems, but it is not rare that nutrient contents and ratios are reported. Although relatively harder to measure, such traits can exert a strong influence on elemental cycling (including nutrient recycling), C sink/burial (mostly in oceans) and other vertical fluxes (when combined with DVM), bacterial activity, and primary productivity, especially in nutrient-poor systems (Frangoulis et al. 2005, Steinberg and Landry 2017, Cavan et al. 2019).

There are multiple examples of how zooplankton excretion and egestion can be used as effect traits, with studies explicitly quantifying the relative contribution of community-weighted traits to

overall C, N and P pools and cycling. For instance, Hernández-León et al. (2008) estimated that the total amount of N-ammonia excreted by mesozooplankton in the oceanic upper layer accounted for approximately 1.78 Gt N per year. In their global analysis, they showed that N inputs derived from mesozooplankton excretion decreased from tropical to polar waters, with the largest contribution to photosynthesis observed in the tropical and subtropical areas, due to temperature-dependence. Globally, nutrient recycling by marine mesozooplankton was estimated to be in the range of 12–23% of the requirements for phytoplankton and bacterial production (Hernández-León et al. 2008). Such contributions can, however, increase in importance in smaller scale assessments; e.g., up to 90% in some marine habitats or even exceeding 100% in oligotrophic freshwater systems (Jawed 1973, Villar-Argaiz et al. 2001).

Elemental or Stoichiometric Body Composition (SURVIVAL/MORTALITY, FEEDING)

Organismal elemental ratios (C:N, C:P or N:P, primarily) are increasingly being referred to as ‘stoichiometric traits’, with likely influences on taxon co-existence, nutrient recycling and growth rate with regards to nutrient limitation (Elser et al. 2000). As opposed to phytoplankton, the stoichiometry of consumers such as zooplankton is homeostatic, making stoichiometric trait values rather “fixed” or static. These ratios capture body requirements and inform on biochemical composition; for example, daphniids are known to have high P requirements, in part due to their greater nucleic acid content (Sternner and Elser 2002). Preferentially storing an element relative to others will influence the stoichiometry of the excretory products (e.g., P-rich daphniids excrete relatively less P), with direct influence on the nutrient balance available to primary producers in the environment. For taxa that are able to select amongst items captured and consumed, their choice of prey can be influenced by their corporal needs.

While species distribution may reflect the signal of habitat filtering, in that some taxa may preferentially be found in habitats that can meet their body requirements, stoichiometric traits primarily operate as effect traits as they dictate diet preferences (for selective feeders), nutrient ratios in excretory products and nutritional value for zooplankton predators. Using stoichiometric traits in food web models can help track C:N:P flow and ratio across trophic levels (Litchman et al. 2013).

Growth Rate (GROWTH/REPRODUCTION)

The maximum growth rate of an organism will determine the degree to which it can respond to environmental variation and will also determine secondary productivity rates of the zooplankton community. Body size will usually be used as a proxy of this rate (often in conjunction with temperature and resource availability). While growing, crustacean zooplankton can moult, with exuviae release contributing to the pool of particulate organic C sinking in the water column (Steinberg and Landry 2017). Organismal growth is a trait that operates at various levels of organization, and can thus be used both as a response trait (e.g., indicator of stressful conditions, such as in nutrient-depleted environments; “growth rate hypothesis”; Sternner and Elser 2002) and as an effect trait, with direct implication for biomass/C stocks comprised in ecosystems (Hébert et al. 2017).

Longevity (SURVIVAL/MORTALITY)

As outlined in the Litchman et al. (2013) framework, longevity is influenced by the degree to which organisms invest in maintenance and repair relative to growth and reproduction. It is also influenced by the degree to which a zooplankter is exposed to predation (which depends on other traits related to predator evasion) and its starvation tolerance. Survivorship, and thus longevity, has not been studied generally enough to date to be a useful trait to distinguish between communities.

Starvation Tolerance (SURVIVAL/MORTALITY)

The ability to survive periods of low prey availability is also likely to differ among metazooplankton, but has not been well studied generally. When present in a community, this response trait may be indicative of higher resistance to stressful conditions, likely capturing signals of habitat filtering. Where it has been examined, it is usually within the context of surviving winter conditions by some freshwater taxa and could therefore be combined with dormancy as an alternative strategy to survive stressful conditions by reducing metabolism (see “dormancy” trait in next section; Ohman et al. 1998). The accumulation of lipid (wax esters) reserves has been identified as a preparation step for winter dormancy in (mostly marine) copepods (Ohman et al. 1998); in freshwaters, however, pre-winter acquisition of algal lipids can support egg production in active overwintering copepods (Schneider et al. 2017). The composition of the lipids stored prior to winter may also be indicative of overwintering strategies; for example, the freshwater cladoceran *Daphnia* retains high levels of polyunsaturated fatty acids to remain active throughout winter (Mariash et al. 2016).

1.2.4 Life History Traits*Reproduction (GROWTH/REPRODUCTION)*

Metazooplankton can display diversity in their reproductive traits. Reproductive mode can vary from asexual to sexual reproduction (including hermaphroditism). Taxa reproducing asexually for most of their life cycle include cladocerans, tunicates, jellyfish (cnidaria) and rotifers while copepods and euphausiids typically reproduce sexually (Paffenhöfer and Harris 1976, Gilbert 1983, Lucas 2000, Decaestecker et al. 2009). Hermaphroditism is common to chaetognaths and some gelatinous metazooplankton like many ctenophores (Chiu 1963, Barnes 1980). Asexual taxa may be advantaged by very high population reproductive rates when resources are plentiful (Gilbert 1983, Decaestecker et al. 2009). Production of dormant stages may occur during harsh periods in certain taxa, which can also be considered a trait (Gilbert 1974).

In terms of investment in embryo development and numbers, some taxa are broadcast spawners (e.g., many euphausiid species), usually when large numbers of eggs containing small embryos are released. Meanwhile, at the other end of the parental investment spectrum, some metazooplankton such as other euphausiid species, cladocerans and copepods carry their eggs for longer, providing greater protection to the smaller number of embryos produced (Hirst and Lopez-Urrutia 2006). These differences in parental investment in metazooplankton also lead to the general trade-off between offspring size and number (r versus K strategies in ecology).

Size at Maturity (GROWTH/REPRODUCTION)

This trait is generally traded-off against reproductive investments: a greater size at maturity represents greater investment in growth relative to reproduction. It will vary across metazooplankton taxa, although a comprehensive comparison across the suite of taxa represented has not been done. Some groups appear to be more plastic in their ability to modify size at maturity relative to reproductive investment (e.g., rotifers) than others (e.g., copepods; Litchman et al. 2013).

Dormancy (SURVIVAL/MORTALITY)

There is variation amongst metazooplankton in their ability to produce dormant resting stages, usually in the form of resistant eggs, enabling survival during periods of low food or sub-optimal environmental conditions. In lakes, some copepods and most cladocerans appear to produce such resting eggs. Cladoceran ephippia may be more resistant than copepods in the long-term, as shown by

the greater success of resurrection ecology experiments with cladocerans and the apparently greater capacity for dispersal of cladocerans than copepods (Louette and DeMeester 2005). Copepods and euphausiids appear to be the dominant groups possessing this trait in marine environments. Bdelloid rotifers can undergo cryptobiosis, a process by which they can survive desiccation for months at a time in very dry environments. Traits embedding zooplankton tolerance and adaptive strategies to cope with stressful conditions can generally be used as response traits.

1.3 Underrepresented Aspects of Trait-based Studies

1.3.1 Traits

While trait-based studies of metazooplankton have increased over the last two decades, some traits have been more studied than others. This results from the cost of measurement, data scarcity in the literature or the limited ecological relevance of a given trait for a specific study. In a recent systematic review aiming to determine which functional traits were most used to characterize cladoceran, copepod and rotifer communities in inland waters, the most frequently used trait was body size (used in 65% of retained publications), closely followed by feeding-related traits and habitat type (Gomes et al. 2019). Similarly, these traits were among the ones for which Hébert et al. (2016b) found the widest taxonomic coverage across habitats types. In their freshwater trait synthesis, however, Barnett et al. (2007) pointed to greater data paucity of information on cyclopoid copepod feeding. In their meta-analysis of “effect” traits in crustacean zooplankton, Hébert et al. (2016a) reported that physiological traits such as excretion and respiration rates as well as stoichiometric traits characterizing C, N and P corporeal content had overall relatively lower taxonomic coverage. Their contention was that this reflected that effect traits are harder to measure and were thus systematically scarcer in the literature. However, it was noted that marine species were more represented in the entirety of the physiological and stoichiometric trait data compiled by Hébert et al. (2016a). This likely reflects a greater focus of oceanographic studies towards zooplankton metabolism and stoichiometry, including their biogeochemical consequences.

1.3.2 Taxa

Functional trait-based approaches to zooplankton communities tend to focus on crustaceans, likely due to their disproportionally high abundance and widespread geographical coverage, transcending both marine and freshwater habitats. In their review, Gomes et al. (2019) reported that 67.5%, 55% and 37.5% of freshwater studies focused on cladocerans, copepods and rotifers, respectively. Although restricted to freshwaters, studies of rotifer traits are less common than for crustaceans, with data being of limited availability for many species (Gsell et al. 2016). Increasing taxonomic coverage in rotifer traits would favour their incorporation in trait-based studies, especially for food web interaction models aiming at reducing overall complexity (Merico et al. 2009). Analogously, trait information on gelatinous forms of zooplankton are mostly restrained to marine studies, with very few gelatinous taxa found in freshwaters. While the trait framework is also less applied to such groups of larger zooplankton, some of their trait values, relationships and patterns along environmental gradients have been relatively well documented outside of the functional trait literature. For example, bell diameter to mass ratios in gelatinous zooplankton (e.g., the scyphomedusa *Aurelia aurita*) vary along salinity levels, which can influence individual buoyancy and mobility (Hirst and Lucas 1998). Another example would include the vertical distribution patterns of pteropods as a function of aragonite saturation, owing to the high sensitivity of their shell to acidification (Bednaršek and Ohman 2015). Although likely rare in the literature, several physiological traits such as excretion rates have been measured for gelatinous zooplankton (Ikeda 1985; note that this study includes several groups of zooplankton). Thus, for underrepresented zooplankton groups and taxa in trait-based

approaches, a key step would be to systematically synthesize this information, as has been done for crustacean species to provide useable databases, but to also identify important lacunae where further trait estimates are needed.

1.3.3 Habitats and Areas

Similar to the way in which some traits may be more represented in marine or freshwater environments, some sub-habitats within ecosystem types may also be differentially studied. For example, limnological studies that focus on lakes and reservoirs often focus much more attention on pelagic species relative to those living in littoral and benthic zones, as shown in Barnett et al. (2007). Similarly, trait information on pelagic metazooplankton from the upper oceanic layer (including coastal areas) tends to be relatively more documented, as opposed to data from the deep-sea or other spatially sparse and more circumscribed habitats (e.g., mangroves, kelp forests). This reveals an important caveat in trait-based studies, given how strongly sub-habitats can constrain trait expression and diversity. For example, in deep waters, marine gelatinous zooplankton have developed particular physio-behavioural strategies to control their luminescence in the absence of light (Haddock and Case 1999); lower temperatures and resource availability also constrain physiological traits, with depth-related declines in respiration and excretion rates being observed in many deep-dwelling crustaceans, such as amphipods, decapods, euphausiids, mysids, and copepods (Ikeda 2014). Furthermore, there are clear knowledge gaps in the geographical coverage at larger scales, such as in the more diverse tropical freshwater areas (de Oliveira Sodr  and Bozelli 2019). For instance, according to the review conducted by Gomes et al. (2019), most trait-based studies were performed in Canada and the U.S., followed by Brazil and Italy. While the number of retained publications may be influenced by the constrained methodologies associated with systematic reviews (i.e., use of specific key words or search engines), this trend reflects previously acknowledged biases in trait data towards other parts of the world (but see Rizo et al. 2017 for a synthesis on Asian cladoceran traits).

1.3.4 Seasons

Finally, another less-studied dimension of trait-based ecology in the study of metazooplankton is the temporal coverage of trait expression and variation, especially in areas where aquatic systems exhibit strong seasonality. While most traits are studied during the so-called growing season, the ecological strategies of organisms thriving in less-studied seasons may be better understood through the study of their traits, especially prior to or during colder and harsher (usually winter) months in temperate areas. For instance, traits related to starvation tolerance or energy storage may allow freshwater metazooplankton to overwinter instead of relying on dormancy to survive the winter months; e.g., as observed in *Daphnia* (Mariash et al. 2016).

1.4 Trait Estimates, Correlations and Trade-Offs

1.4.1 Direct Measurement

Metazooplankton traits have been increasingly measured and reported in recent years. According to Gomes et al. (2019), roughly half of the trait-based studies on freshwater zooplankton to date directly measured observations, whereas the other half used literature-based values. Although using published taxon-specific trait estimates instead of species identity in analyses can help uncover relationships that could not be revealed otherwise, using trait values that have been estimated under different environmental conditions than those under study may mask or bias site-specific ecological linkages. This is especially the case for highly-plastic, stress-related or habitat-constrained traits, where trait values can greatly vary even within species. That said, if the species included in a

study span various groups of zooplankton that typically express reasonable variability in the traits of interest (e.g., body size across rotifers, copepods, amphipods), using literature-based estimates may still enable the detection of functional patterns. When assessing traits expressed in closely related species or when it is impossible to directly measure traits, using less-variable (i.e., fixed or static) traits from the literature may be more suitable and easily transportable across study systems (e.g., zooplankton body stoichiometry; see Section 1.6 for a study example by Moody and Wilkinson 2019).

1.4.2 Estimates and Correlations in Quantitative Traits

There are still many knowledge gaps, especially for quantitative traits in the literature. Thus, generating more data on underrepresented traits and taxa is an obvious recommendation to help move the field forward, as highlighted in Section 3. However, an alternative approach is the use of soft traits or predictive equations to estimate unmeasured trait values based on known relationships (Nock et al. 2016).

Although less mechanistically correlated with precise functions of interest, more readily measurable soft traits can sometimes be used as surrogate metrics to infer hard traits. Because it transcends multiple organismal functions, the most common soft trait is consistent body size. Allometric equations that describe the scaling relationships between organismal size and individual-level biological variables, such as morphological features or metabolic rates, have been extensively developed for zooplankton (Hébert et al. 2017, Arhonditsis et al. 2019). Developing such equations is a powerful means towards generalizing trait relationships, further facilitating the estimation of unknown trait values. A non-exhaustive, though representative, list of morphological, physiological and life-history allometric relationships commonly used for marine and/or freshwater zooplankton is provided in Table 1 from Arhonditsis et al. (2019).

Mass-length equations are often used to infer body mass based on length given that the latter is much easier to measure than the former, enabling the estimation of overall taxon or community biomass when combined with abundance data. Allometric exponents can differ across taxa, including among crustacean taxonomic sub-groups owing to differences in body shapes; e.g., copepods versus daphniid-like cladocerans versus smaller, rounder cladocerans such as Bosminidae or Chydoridae (Hébert et al. 2016a). Such exponents can also vary considerably within genera or species (McCauley 1984); in some cases, they can even be habitat-specific (see Section 1.5; Hébert et al. 2016a). Care should be taken, however, not to extrapolate trait estimates based on size falling outside of the size spectrum covered by established relationships; McCauley et al. (1984) offer an extensive set of species-specific mass-length equations with the associated size ranges of application. A further step in the use of allometry in ecosystem models is to combine mass-length equations and mass-scaled exponents of physiological traits to estimate a community's contribution to a particular ecosystem level process based on organismal body lengths alone (Hébert et al. 2017).

Well-established relationships between body mass and physiological rates can also help estimate hard trait values. There is a wide variety of studies (mostly on marine zooplankton) providing general models to estimate excretion, respiration, growth, fecundity or clearance rates (Ikeda 1985, Hirst and Lampitt 1998, Ikeda et al. 2001, Barnett et al. 2007, Kiørboe and Hirst 2014, Hébert et al. 2016a). For example, Ikeda et al. (2001) have shown that body mass and temperature alone could explain on average 94%, 77% and 51% of the variation in respiration, ammonia, and phosphate excretion rates, respectively, in epipelagic marine copepods along large latitudinal gradients. When corrected for temperature, metabolic or physiological rates theoretically scale with body mass to the $3/4$ power (or $-1/4$ on a mass-specific basis). This mass-scaled exponent refers to the general power law in ecology (Kleiber 1961, Peters 1983) and has been derived from large datasets on various animal classes. When experimentally measured on a more constrained group of organisms, however, scaling exponents can considerably diverge from theory, and the use of taxon- and process-specific

exponents is recommended. For example, Hébert et al. (2016a) reported exponents of 0.70 and 0.84 for the mass dependency of P and N excretion rates, respectively, of crustacean zooplankton; despite the discrepancy, both mass-scaled exponents are within ranges of values observed in other nutrient excretion studies, with exponents for N excretion being typically higher. Furthermore, the use of scaling exponents derived from very large size spectra to make such estimations should also be avoided, as it includes a greater degree of uncertainty (Glazier 2006).

Stoichiometric traits can also be used to estimate other biological parameters. For excretion and egestion, the balance between corporeal and resource N:P ratios is often used to project nutrient ratios in excreted and egested products (Elser and Urabe 1999). When both respiration and excretion rates are measured, the ratio of oxygen (O) respired to N-ammonia excreted (O:N) can also be used as an indicator of the primary substrates (proteins versus lipids) for metabolism, with that of zooplankton from temperate and subpolar areas being typically more lipid-based due to energy storage in colder regions (Hernández-León et al. 2008).

1.4.3 Trade-Offs

Identifying trait trade-offs can help reveal ecological strategies amongst metazooplankton, with regards to fitness optimization under different environmental conditions. Organismal fitness is achieved by allotting energy amongst different fundamental functions: survival, growth, reproduction and feeding. As pointed out in Section 1.2, traits can be classified into these components, and trade-offs may occur between inter-related traits from different categories.

Strong trait trade-offs related to morphology, behaviour, and feeding can be found across multiple zooplankton taxa, with common examples including trade-offs between resource acquisition/competition versus defence, feeding versus hiding, prey size versus prey selection (Gliwicz 2003, Yoshida et al. 2003, Kiørboe 2011). Some traits can also be related to strategies under stressful or more harsh environmental conditions, with a trade-off that can be imposed between starvation tolerance (survival) and delayed reproduction, as observed in copepods, jellyfish and pteropods (Litchman et al. 2013). Investment in energy storage or tissue repair may enhance longevity, but this leaves less energy for growth and reproduction. More generally, there is a trade-off between growth and reproductive success (Section 1.2). However, trade-offs can also occur between traits related to a single organismal function, such as growth, with investment in growth rate during early ontogenetic stages likely reducing size at maturity- a trade-off that can be modulated by temperature (Gillooly et al. 2002).

Many trade-offs can be associated with mobility given that swimming increases the risk of encountering both prey and mates, but also predators. While searching for prey or mates is beneficial for feeding and reproduction, respectively, swimming can trigger fluid disturbances in marine copepods that may be detected by rheotactic predators, reducing survival (Kiørboe 2008). Performing vertical migration to evade predators also implies lost feeding opportunities (Kiørboe 2011). Such motility-related trade-offs illustrate well how it is impossible for organisms to simultaneously optimize all fundamental activities.

1.5 Variation in Traits between Freshwater and Marine Environments

Examining trait distribution across aquatic ecosystems can provide valuable insight into the drivers shaping community structure. There are inherent differences between traits from marine and freshwater metazooplankton, in large part owing to habitat constraints. One stark contrast is the much greater taxonomic diversity in marine environments compared to freshwaters, which can lead to the quasi-exclusive presence of certain traits in marine ecosystem type (e.g., metazoan bioluminescence). In contrast, seasonality can often be more pronounced in freshwater relative to marine systems, making some traits relatively more important than others for zooplankton life history strategies, such as traits

related to reproduction and dormancy. While there are discrepancies in the amount of information that has been reported in marine versus freshwater studies (see Section 1.3), there are trait values and relationships that can vary considerably between ecosystem types.

1.5.1 Trait Values

As reported in Hébert et al. (2016a), marine crustacean zooplankton have significantly larger body sizes, with 2-fold greater body length and 7-fold greater dry mass than freshwater species. Meanwhile, with respect to corporeal composition, although %C and %N body content seem to be similar across marine and freshwater crustaceans, %P and N:P ratios are systematically higher and lower, respectively, in freshwater species. This is in large part due to the known high P requirements in freshwater cladocerans, especially daphniids. Analogously, N:P ratios in the excreted products of freshwater cladocerans, especially for daphniids, are expected to be much higher than any marine taxa (Sterner and Elser 2002). In terms of physiological traits, based on the data compilation provided in Hébert et al. (2016b), mass-scaled rates of respiration and N and P excretion in crustaceans are all higher (3x, 2.5x and 5.5x, respectively) in freshwater representatives, suggesting overall higher metabolic activity in freshwater zooplankton likely due to environmental constraints (e.g., food supply, higher temporally constrained seasons).

1.5.2 Trait Relationships

When comparing allometry in crustaceans, Hébert et al. (2016a) showed that marine species may be heavier at equivalent body length, and may also gain more mass as they increase in length than do those in freshwater habitats. This pattern was not only found across all taxa, but also within taxa, with a 4-fold difference between marine and freshwater calanoids. Because of this, variation in general body shape of dominant taxa (predominantly copepods in marine ecosystems and relatively more cladocerans in freshwaters) cannot explain this pattern, nor can phylogeny exclusively; rather, this could be hypothetically due to habitat-constrained adaptive differences such as the need to control buoyancy in saltwater when performing vertical migration for example. Irrespective of causes, few, if any, studies have compared crustacean body tissue density between these major aquatic ecosystems.

Another striking difference between ecosystem types is the 3-fold higher mass-specific respiration rates in freshwater zooplankton (Hébert et al. 2016a). A similar observation can be made when inspecting the observed versus predicted values of crustacean respiration in the study by Hernández-León and Ikeda (2005) in which observed respiration rates in marine copepods were systematically lower than that predicted by their general model based on body mass and temperature alone. While this divergence in respiration may require further investigation before confirming any pattern, potential ecological explanations could include greater cost associated with osmoregulation or life-history strategies related to differential investment in growth and reproduction. Potentially more productive and seasonally constrained freshwater habitats may induce higher metabolic activity in zooplankton, in contrast to marine environments where food supply can sometimes be consistently scarcer.

1.6 Functional Diversity in Metazooplankton Communities

Once a set of traits can be attributed to a community of plankton, it is possible to investigate the functional ecology of this community in greater detail. The advantage of a trait-based approach is that it brings mechanistic understanding to our examination of communities, including how their ecological role may vary through time and space. For example, Barnett and Beisner (2007) used their trait matrix for eastern North American freshwater zooplankton to examine how functional trait diversity varied along nutrient (P) gradients in lakes. The trait-based approach demonstrated a

linear decline in functional diversity with lake enrichment, even though taxonomic diversity (species richness) demonstrated the expected unimodal (hump-shaped) relationship. This difference suggests that oligotrophic lakes, whilst having relatively low species richness, possess communities with very high functional diversity, enabling these communities to harness resources and use survival mechanisms in a variety of ways. On the other hand, nutrient-enriched lakes, also showing low species richness, were made up of relatively similar organisms with respect to their traits, and thus less likely to be resilient to future perturbations to the ecosystem should they arise. This novel hindsight could only be gained through a trait-based approach.

There is now a wide variety of zooplankton traits that have been identified, with trait data sets being increasingly made available, as pointed out in this chapter. However, all traits may not be equally useful to derive functional diversity indices, especially if the goal is to determine relationships between such indices and particular ecological parameters (e.g., related to ecosystem functioning). Therefore, care should be taken when choosing traits to consider in a study (see Section 1.7; Petchey and Gaston 2002). Further, if traits are not directly observed on organisms but are rather literature-based taxon-specific values, static/fixed traits may be more suitable and easily transposable to various study systems given that they may be less responsive to environmental variability (Section 1.4). One example of relatively fixed traits is the stoichiometric composition of zooplankton bodies. For instance, Moody and Wilkinson (2019) used stoichiometric traits compiled by Hébert et al. (2016b) to examine functional and taxonomic diversity variation in lake zooplankton communities along nutrient gradients. In accordance with Barnett and Beisner (2007), they also found that functional dispersion decreased with P-load, but using literature-based, fixed, stoichiometric traits. Their study showed that stoichiometric trait distributions in lake zooplankton shifted with eutrophication, with high N:P ratio organisms increasing in abundance with lake P-levels. Higher dominance of P-poor individuals also indicate that zooplankton communities may have exacerbated the high supply of P in hypertrophic lakes by excreting more P relative to N, suggesting a potential contribution of zooplankton to the eutrophication process in lakes.

Generally, functional diversity has been used in two main contexts. The first is in the context of what has been entitled “assembly rules” in ecology, i.e., what are the patterns in community composition, and what are the environmental factors that affect these. Barnett and Beisner (2007) and Vogt et al. (2013) provide examples of this use of functional trait diversity applied to zooplankton across a landscape of lakes. As discussed in Section 1.2, traits in this context are mainly considered to be response traits with respect to the environment or habitat constraints. The second context is geared towards ecosystem level functional consequences, within which traits are considered to reflect what organisms in a community do in order to affect ecosystem stocks and fluxes (effect traits).

With respect to the response-effect trait framework, the idea is that functional diversity indices capture complementarity and redundancy in a community, and should allow for greater explanatory power with respect to the role of organisms in ecosystems than does the sole number of species (richness), as has frequently been used in diversity–ecosystem functioning relationships. In some cases, species richness and functional diversity can be linearly related (Box 1.1; Fig. 1.1A), while communities that are composed of functionally redundant species exhibit lower functional diversity regardless of the number of species (Box 1.1; Fig. 1.1B), which may result in reduced ecosystem processing if indices are based on effect traits (Box 1.1; Fig. 1.1C versus 1.1D). Particularly relevant in the face of environmental change, greater functional diversity in response traits may allow overall communities to persist despite species loss or sorting, thereby favouring stability (Box 1.1; Fig. 1.2A), whereas functional redundancy in effect traits may exert stabilizing effects on ecosystem processes (Box 1.1; Fig. 1.2B). Functionally equivalent species in terms of their contribution to ecosystem processes (i.e., low to moderate effect trait diversity; functional redundancy) can compensate for the loss of other species (insurance hypothesis) or dampen the effects of species abundance fluctuations (portfolio effect; Box 1.1; Fig. 1.1E versus 1.1F), hence providing greater ecosystem stability (Fig. 1.2B; Rosenfield 2002, Thibaut and Connolly 2013). In this context, assessing the functional

Box 1.1: Relationships between functional diversity, species richness, ecosystem processes and ecosystem stability.

In biodiversity research, it is often assumed that functional diversity is linearly related to ecosystem processing (Fig. 1.1C-D). The linearity of this relationship, however, is independent of that between taxonomic and functional diversity (Fig. 1.1A-B), the latter being entirely dictated by community composition. For a given (fixed) number of species, a set of functionally complementary traits results in greater functional diversity indices (Fig. 1.1A), while functionally redundant traits translate into lower functional diversity indices (Fig. 1.1B), with potentially relatively less ecosystem processing achieved (Fig. 1.1D). Differential relationships between taxonomic and functional diversity (reflecting functional complementarity or redundancy; Fig. 1.1A versus 1.1B, respectively) can be indicative of how species richness may influence ecosystem processes (Fig. 1.1E versus 1.1F, respectively). Regardless of the degree to which ecosystem processes are realized (Y axis in Fig. 1.1C-D-E-F), if the response of a community exposed to environmental changes or stressors is the loss of species, then the supposedly negative impact on ecosystem processes will be greater in communities with high functional complementarity (Fig. 1.1E) relative to those composed of functionally redundant species (Fig. 1.1F). Diminished impacts of species loss on ecosystem processing through functional redundancy, however, implies that functional diversity is evaluated on the basis of effect traits that regulate key ecosystem control functions.

A common assumption in community ecology is that communities exhibiting a high diversity of response traits may persist under changing or stressful conditions, with assembly mechanisms regulating fluctuations in relative abundances of species based on their response trait optimum ranges. For example, greater functional diversity in a pool of response traits related to thermal affinities or tolerance to starvation or hypoxia may allow community biomass to remain stable despite a change in species relative abundances or richness. From that perspective, greater functional complementarity in response traits may confer greater stability (Fig. 1.2A). Species sorting or loss may, however, be detrimental to ecosystem processing, if key functions can no longer or can only be partly fulfilled due to the loss or reduced presence of some effect traits (e.g., reduced grazing pressure may alter water clarity and thus quality). In such cases, functional redundancy in effect traits may help maintain a certain level of ecosystem processing, with functionally equivalent species compensating for the loss (insurance hypothesis) or lower abundance (portfolio effect) of other species (Rosenfield 2002, Thibaut and Connolly 2013); communities with low or moderate effect trait diversity may thus exert stabilizing effects on ecosystems (Fig. 1.2B). In this context, zooplankton communities with a high diversity of response traits (Fig. 1.2A) but a relatively moderate diversity of effect traits (Fig. 1.2B) may be the most beneficial for the stability and resilience of aquatic ecosystems.

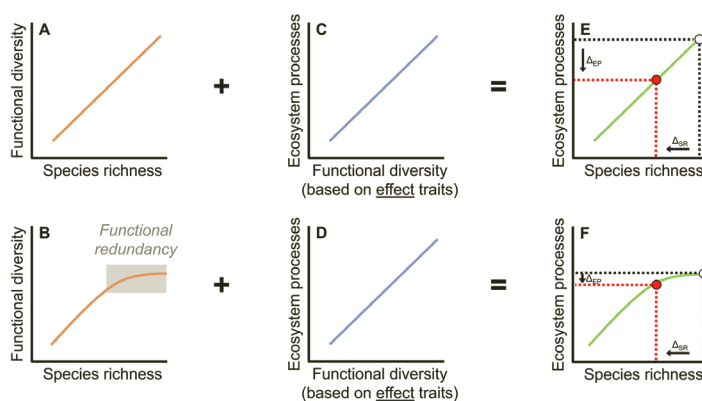


Figure 1.1: Predicted relationships between species richness, functional diversity and ecosystem processes based on biodiversity–ecosystem functioning principles. Panels from the first row (A-D-E) versus the second row (B-D-F) refer to different scenarios of community composition: greater functional complementarity (row 1; A) versus greater functional redundancy (row 2; B). Together, these scenarios indicate how the presumably negative impact of species loss (reducing species richness; transition from the white to the red circle on the horizontal axis; Δ_{SR}) on ecosystem processes (reducing ecosystem processing; transition from the white to the red circle on the vertical axis; Δ_{EP}) can be mediated by functional redundancy in effect trait diversity (B-F; as opposed to A-E) (Adapted from Petchey and Gaston 2006).

Box 1.1 contd. ...

...Box 1.1 contd.

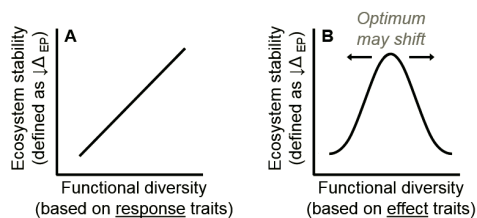


Figure 1.2: Differential relationships between functional diversity in response (A) versus effect (B) traits and ecosystem stability. Ecosystem stability is defined as the magnitude of change in ecosystem processes (Δ_{EP}), with small to no changes in ecosystem processing associated with greater stability. Note that for the relationship between functional effect trait diversity and ecosystem stability (B), the optimum value may be context-dependant, potentially resulting in either hump-shaped, left-skewed or right-skewed relationships.

diversity of species effect traits can not only provide insight into the role of communities in ecosystem functioning, but also how they may confer stability and resilience at higher levels of organization (McNaughton 1977, Hooper et al. 2005).

Over the past decade, a plethora of indices have been developed to estimate functional diversity based on accentuating the various components of diversity (richness and evenness or their combination) to differing degrees. Schleuter et al. (2010) gives an excellent overview of the most commonly used functional trait diversity indices, including those of Villéger et al. (2008): functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional diversity FD. To that, the functional dispersion (FDis) indicator developed by Laliberté and Legendre (2010) can be added. The FD package in R that accompanied the publication of Villéger et al. (2008) can be used to estimate these common diversity indices. In a general sense, functional diversity indices reflect different methods to estimate the way in which the composition of a community statistically “fills” a multivariate trait space: in degree (how much trait-space is covered by different traits; analogous to richness), type (which traits are most represented; analogous to evenness) or both (analogous to diversity).

In addition to constraining the set of traits used to those that reflect the ecological question of interest, another important consideration when calculating functional diversity is the number of traits to include (Petchey and Gaston 2006). Even if multiple traits could be considered relevant to a study, there is a natural limit as including too many traits will reduce any estimate of diversity back to the same as species richness: each species has a unique set of traits when too many are considered. Alternatively, one can try all combinations of traits to search for the best overall combination that corresponds to the gradient of interest, as done in Barnett and Beisner (2007)—analogous to using variable transformations to find the best regression for a study and maximize the variation explained in a dataset. Finally, it is also possible to weigh traits differently such that traits that are highly correlated, for example, can be down-weighted relative to more distinct traits that are not correlated. More general or theoretical publications further elaborate on the steps to follow when using multiple traits in functional diversity research (Lefcheck et al. 2015).

1.7 Remarks and Recommendations for Future Trait-based Approaches

Akin to other subfields of ecology and organism types, the increasing interest in trait-based approaches to describe metazooplankton has fostered a multi-scale framework using species responses and effects within a tropho-dynamic and evolutionary context, with regard to ecological forecast under scenarios of global change (Diaz et al. 2007). The growing body of work on metazooplankton trait distributions along various environmental gradients (e.g., of human activity,

or latitude/temperature) has advanced our understanding of how environmental factors influence community assembly processes and feedback with ecosystem functioning, generating knowledge that can then be used to make future predictions. Generating more trait data would improve our ability to quantify and parametrize intra- and inter-specific trait variation, correlation and trade-offs in ecosystem models of static or dynamic environments. Syntheses and assemblages of comprehensive trait databases in recent years have greatly facilitated the development of trait-based studies; however, there are still many gaps in the reported or modelled trait information available for metazooplankton. As previously advocated in this chapter and in other studies, an obvious recommendation for the advancement of this field would be for more trait measurements and data disclosure, especially for under-represented traits, taxa, habitat types and areas. Then, developing, calibrating, and validating modelling techniques to infer trait values based on phylogeny (Bruggemann 2011), known trait relationships or response to particular environmental factors such as temperature (Robson et al. 2018) can help facilitate the implementation of functional traits into zooplankton community characterizations.

As the field of trait-based ecology moves forward, a notional, though not trivial, step that should be reinforced when deriving trait-based community descriptors is to meaningfully consider which traits to incorporate in a study. Although often constrained by data availability or the cost and time associated with acquiring new observations, the selection of traits should primarily rely on study objectives. Identifying which traits are most relevant remain a challenge in ecology; for example, choosing which traits should be included in biodiversity-ecosystem functioning relations can be difficult, given that many traits can interact or synergistically influence different aspects of ecosystem functioning (Hooper et al. 2005). In such cases, using traits that are not directly related to the ecological parameters of interest may introduce bias into analyses, hampering the detection or quantification of ecological linkages. Furthermore, clearly defining goals with respect to the rationale for the choice of traits may facilitate trait selection for future studies addressing similar questions, enabling more direct comparisons of how particular trait assemblages may vary in different contexts.

The integrative nature of trait-based approaches has thus far contributed to consolidate ecological information on metazooplankton from various studies that are largely outside of the functional ecology literature. In addition to permitting comparative assessments of metazooplankton features across types of aquatic environments, the use of traits can also help to gain a more generalized understanding of how whole food webs are structured, from the base of the food web to top consumers. For example, already documented information on diet variety, food size ranges or the frequency distribution of ingested food particles could be included in food web interaction models (Gsell et al. 2016). Incorporating stoichiometric traits of consumers and prey when representing food web interactions can also provide insight as to how elemental stocks are structured and flow across trophic levels (Sterner and Elser 2002). In ecosystem models, the inclusion of feeding and stoichiometric traits, along with physiological trait measurements such as growth, respiration or excretion rates would advance our ability to quantify organismal contributions to ecosystem storage and fluxes. Ultimately then, consideration of zooplankton communities by their functional traits can help better characterize the roles, with respect to other environmental drivers, of organisms in aquatic food webs and in ecosystem processing, including biogeochemical cycling.

References

- Arhonditsis, G.B., Y. Shimoda and N.E. Kelly. 2019. Allometric theory: extrapolations from individuals to ecosystems. *Encyclopedia of Ecology* (2nd Edition), Elsevier 2: 242–255.
- Aristegui, J., C.M. Duarte, I. Reche and J.L. Gomez-pinchetti. 2014. Krill excretion boosts microbial activity in the Southern Ocean. *PLoS ONE* 9: e89391.
- Barneche, D., M. Kulbicki, S. Floeter, A. Friedlander, J. Maina and A.P. Allen. 2014. Scaling metabolism from individuals to fish communities at broad spatial scales. *Ecol. Lett.* 17: 1067–1076.
- Barnes, R.D. 1980. *Invertebrate Zoology*. Philadelphia: W. B. Saunders Coll.
- Barnett, A.J. and B.E. Beisner. 2007. Zooplankton biodiversity and primary productivity: explanations invoking resource abundance and distribution. *Ecology* 88: 1675–1686.

- Barnett, A.J., K. Finlay and B.E. Beisner. 2007. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biol.* 52: 796–813.
- Bednaršek, N. and M.D. Ohman. 2015. Changes in pteropod distributions and shell dissolution across a frontal system in the California Current System. *Mar. Ecol. Prog. Ser.* 523: 93–103.
- Benedetti, F., S. Gasparini and S.-D. Ayata. 2015. Identifying copepod functional groups from species functional traits. *J. Plankton Res.* 38: 159–166.
- Bode, M., A. Schukat, W. Hagen and H. Auel. 2013. Predicting metabolic rates of calanoid copepods. *J. Exp. Mar. Biol. Ecol.* 444: 1–7.
- Boltovskoy, D. and N.M. Correa. 2021. Planktonic shelled protists (Foraminifera and Radiolaria Polycystina): Global biogeographic patterns in the surface sediments. pp. 119–141. *In: M.A. Teodósio and A.B. Barbosa [eds.]. Zooplankton Ecology.* CRC Press.
- Bruggeman, J. 2011. A phylogenetic approach to the estimation of phytoplankton traits. *J. Phycol.* 47: 52–65.
- Brun, P., M.R. Payne and T. Kiørboe. 2016. Trait biogeography of marine copepods—an analysis across scales. *Ecol. Lett.* 19: 1403–1413.
- Burks, R.L., D.M. Lodge, E. Jeppesen and T.L. Lauridsen. 2002. Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. *Freshwater Biol.* 47: 343–365.
- Burrows, M.T., A.E. Bates, M.J. Costello, M. Edwards, G.J. Edgar, C.J. Fox et al. 2019. Ocean community warming responses explained by thermal affinities and temperature gradients. *Nat. Clim. Change* doi.org/10.1038/s41558-019-0631-5.
- Buskey, E.J., P.H. Lenz and D.K. Hartline. 2002. Escape behavior of planktonic copepods to hydrodynamic disturbances: high speed video analysis. *Mar. Ecol. Prog. Ser.* 235: 135–146.
- Buskey, E.J., P.H. Lenz and D.K. Hartline. 2011. Sensory perception, neurobiology, and behavioral adaptations for predator avoidance in planktonic copepods. *Adapt. Behav.* 20: 57–66.
- Cavan, E.L., A. Belcher, A. Atkinson, S.L. Hill, S. Kawaguchi, S. McCormack et al. 2019. The importance of Antarctic krill in biogeochemical cycles. *Nat. Commun.* 10: 4742.
- Chen, B., S.L. Smith and K.W. Wirtz. 2018. Effect of phytoplankton size diversity on primary productivity in the North Pacific: trait distributions under environmental variability. *Ecol. Lett.* 22: 56–66.
- Chiu, S.Y. 1963. On the metamorphosis of the ctenophore *Ocyropsis crystallina* (Rang) from Amoy. *Acta Zool. Sinica* 15: 10–16.
- Conley, K.R., F. Lombard and K.R. Sutherland. 2018. Mammoth grazers on the ocean's minuteness: a review of selective feeding using mucous meshes. *Proc. R. Soc. B* 285: 20180056.
- Costello, J.H., S.P. Colin, B.J. Gemmell, J.O. Dabiri and K.R. Sutherland. 2015. Multi-jet propulsion organized by clonal development in a colonial siphonophore. *Nat. Commun.* 6: 8158.
- Cummins, K.W. and M.J. Klug. 1979. Feeding ecology of stream invertebrates. *Annu. Rev. Ecol. Evol. S.* 10: 147–172.
- Daufresne, M., K. Lengfellner and U. Sommer. 2009. Global warming benefits the small in aquatic ecosystems. *P. Natl. Acad. Sci. USA* 106: 12788–12793.
- Decaestecker, E., L. de Meester and J. Mergeay. 2009. Cyclical parthenogenesis in *Daphnia*: Sexual versus asexual reproduction. pp. 295–316. *In: Lost Sex: The Evolutionary Biology of Parthenogenesis.* Springer.
- DeMott, W.R. and K.W. Kerfoot. 1982. Competition among cladocerans: nature of the interaction between *Bosmina* and *Daphnia*. *Ecology* 63: 1949–1966.
- DeMott, W. and M.D. Watson. 1991. Remote detection of algae by copepods: responses to algal size, odours, and motility. *J. Plankton Res.* 13: 1203–1222.
- Díaz, S., S. Lavorel, F. de Bello, F. Quétier, K. Grigulis and M.T. Robson. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *P. Natl. Acad. Sci. USA* 104: 20684–20689.
- Diéguez, M. and E. Balseiro. 1998. Colony size in *Conochilus hippocrepis*: defensive adaptation to predator size. *In: E. Wurdak, R. Wallace and H. Segers [eds.]. Rotifera VIII: A Comparative Approach.* Developments in Hydrobiology, Vol. 134. Springer, Dordrech.
- Elser, J.J. and J. Urabe. 1999. The stoichiometry of consumer–driven nutrient recycling: theory, observations, and consequences. *Ecology* 80: 735–751.
- Elser, J.J., R.W. Sterner, E. Gorokhova, W.F. Fagan, T.A. Markow, J.B. Cotner et al. 2000. Biological stoichiometry from genes to ecosystems. *Ecol. Lett.* 3: 540–550.
- Frangoulis, C., E.D. Christou and J.H. Hecq. 2005. Comparison of marine copepod outfluxes: nature, rate, fate and role in the carbon and nitrogen cycles. *Adv. Mar. Biol.* 47: 254–309.
- Gauld, D.T. 1951. The grazing rate of planktonic copepods. *J. Mar. Biol. Ass. U.K.* 29: 695–706.
- Gilbert, J.J. 1974. Dormancy in rotifers. *Trans. Am. Microsc. SOC.* 93: 490–513.
- Gilbert, J.J. 1980. Observations on the susceptibility of some Protists and rotifers to predation by *Asplanchna Girodi*. *In: H.J. Dumont and J. Green [eds.]. Rotatoria.* Developments in Hydrobiology, Vol. 1 Springer, Dordrecht.

- Gilbert, J.J. 1983. Rotifera. pp. 181–209. *In*: K.G. Adiyodi and R.G. Adiyodi [eds.]. *Reproduction Biology of Invertebrate: I. Oogenesis, Ovoposition and Oosorption*. John Wiley & Sons, New York, NY.
- Gilbert, J.J. 1985. Escape response of the rotifer *Polyarthra*: a high-speed cinematographic analysis. *Oecologia* 66: 322–331.
- Gillooly, J.F., E.L. Charnov, G.B. West, V.M. Savage and J.H. Brown. 2002. Effects of size and temperature on developmental time. *Nature* 417: 70–73.
- Glazier, D.S. 2006. The 3/4-power law is not universal: evolution of isometric, ontogenetic metabolic scaling in pelagic animals. *BioScience* 56: 325–332.
- Gliwicz, Z.M. 2003. Between hazards of starvation and risk of predation: The ecology of offshore animals. International Ecology Institute, Nordbunte, Germany.
- Gomes, L.F., H.R. Pereira, A.C.A. Missias Gomes, M. Carvalho Vieira, P. Ribeiro Martins, I. Roitman et al. 2019. Zooplankton functional-approach studies in continental aquatic environments: a systematic review. *Aquat. Ecol.* 53: 191–203.
- Grosbois, G. and M. Rautio. 2018. Active and colorful life under lake ice. *Ecology* 99: 752–754.
- Gsell, A., D. Özkundakci, M.P. Hébert and R. Adrian. 2016. Quantifying change in pelagic plankton network stability and topology based on empirical long-term data. *Ecol. Indic.* 65: 76–88.
- Haddock, S.H.D. 2007. Comparative feeding behavior of planktonic ctenophores. *Integr. Comp. Biol.* 47: 847–853.
- Haddock, S. and J. Case. 1999. Bioluminescence spectra of shallow and deep-sea gelatinous zooplankton: ctenophores, medusae and siphonophores. *Mar. Biol.* 133: 571–582.
- Hébert, M.P., B.E. Beisner and R. Maranger. 2016a. A meta-analysis of zooplankton functional traits influencing ecosystem function. *Ecology* 97: 1069–1080.
- Hébert, M.P., B.E. Beisner and R. Maranger. 2016b. A compilation of quantitative functional traits for marine and freshwater crustacean zooplankton. *Ecology* 97: 1081.
- Hébert, M.P., B.E. Beisner and R. Maranger. 2017. Linking zooplankton communities to ecosystem functioning: toward an effect-trait framework. *J. Plankton Res.* 39: 3–12.
- Hernández-León, S. and T. Ikeda. 2005. Zooplankton respiration. pp. 57–82. *In*: P.A. del Giorgio and P. le B. Williams [eds.]. *Respiration in Aquatic Ecosystems*. Oxford University Press, Oxford, UK.
- Hernández-León, S., C. Fraga and T. Ikeda. 2008. A global estimation of mesozooplankton ammonium excretion in the open ocean. *J. Plankton Res.* 30: 577–585.
- Herring, P.J. 1985. Bioluminescence in the Crustacea. *J. Crustacean Biol.* 5: 557–573.
- Hinde, R.T. 1998. The Cnidaria and Ctenophora. pp. 28–57. *In*: D.T. Anderson [ed.]. *Invertebrate Zoology*. Oxford University Press.
- Hirst, A.G. and R.S. Lampitt. 1998. Towards a global model of *in situ* weight-specific growth in marine planktonic copepods. *Mar. Biol.* 132: 247–257.
- Hirst, A.G. and C.H. Lucas. 1998. Salinity influences body weight quantification in the scyphomedusa *Aurelia aurita*: important implications for body weight determination in gelatinous zooplankton. *Mar. Ecol. Prog. Ser.* 165: 259–269.
- Hirst, A. and A. Lopez-Urrutia. 2006. Effects of evolution on egg development time. *Mar. Ecol. Prog. Ser.* 326: 29–35.
- Hodgson, J.G., P.J. Wilson, R. Hunt, J.P. Grime and K. Thompson. 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* 85: 282–294.
- Hooper, D.U., F.S. Chapin, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel et al. 2005 Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75: 3–35.
- Hylander, S., N. Larsson and L.A. Hansson. 2009. Zooplankton vertical migration and plasticity of pigmentation arising from simultaneous UV and predation threats. *Limnol. Oceanogr.* 54: 483–491.
- Ikeda, T. 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. *Mar. Biol.* 85: 1–11.
- Ikeda, T., Y. Kanno, K. Ozaki and A. Shinada. 2001. Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Mar. Biol.* 139: 587–596.
- Ikeda, T. 2014. Respiration and ammonia excretion by marine metazooplankton taxa: synthesis toward a global-bathymetric model. *Mar. Biol.* 161: 2753–2766.
- Jawed, M. 1973. Ammonia excretion by zooplankton and its significance to primary productivity during summer. *Mar. Biol.* 23: 115–120.
- Jiménez-Guri, E., H. Philippe, B. Okamura and P.W. Holland. 2007. *Buddenbrockia* is a Cnidarian Worm. *Science* 317: 116–118.
- Johnsen, S. 2005. The red and the black: Bioluminescence and the color of animals in the deep sea. *Integr. Comp. Biol.* 45: 234–246.

- Jumars, P.A., D.L. Penry, J.A. Baross, M.J. Perry and B.W. Frost. 1989. Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. *Deep-Sea Res.* 36: 483–495.
- Kabata, Z. 1982. Copepoda (Crustacea) parasitic on fishes: problems and perspectives. *Adv. Parasit.* 19: 1–71.
- Keck, B.P., Z.H. Marion, D.J. Martin, J.C. Kaufman, C.P. Harden, J.S. Schwartz et al. 2014. Fish functional traits correlated with environmental variables in a temperate biodiversity hotspot. *PLoS ONE* 9: e93237.
- Kelly, T.B., P.C. Davison, R. Goericke, M.R. Landy, M.D. Ohman and M.R. Stukel. 2019. The importance of mesozooplankton diel vertical migration for sustaining a mesopelagic food web. *Front. Mar. Sci.* Doi: 10.3389/fmars.2019.00508.
- Kenitz, K.M., A.W. Visser, M.D. Ohman, M.R. Landry and K.H. Andersen. 2018. Community trait distribution across environmental gradients. *Ecosystems* 22: 968–980.
- Kjørboe, T. 2008. Optimal swimming strategies in mate-searching pelagic copepods. *Oecologia* 155: 179–192.
- Kjørboe, T. 2011. How zooplankton feed: mechanisms, traits and trade-offs. *Biol. Rev.* 86: 311–339.
- Kjørboe, T. and A.G. Hirst. 2014. Shifts in mass scaling of respiration, feeding, and growth rates across life-form transitions in marine pelagic organisms. *Am. Nat.* 183: E118–E130.
- Kleiber, M. 1961. *The Fire of Life: An Introduction to Animal Energetics*. Wiley, New York, USA.
- Liberté, E. and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.
- Lampert, W. 2005. Vertical distribution of zooplankton: density dependence and evidence for an ideal free distribution with costs. *BMC Biol* 3: 10 Doi: 10.1186/1741-7007-3-10.
- Lankford, T.E., J.M. Billerbeck and D.O. Conover. 2001. Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in *menidia menidia*. *Evolution* 55: 1873–1881.
- Lavorel, S. and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16: 545–556.
- Lefcheck, J.S., V.A. Bastazini and G. Griffin. 2015. Choosing and using multiple traits in functional diversity research. *Environ. Conserv.* 42: 104–107.
- Litchman, E. and C.A. Klausmeier. 2008. Trait-based community ecology of phytoplankton. *Annu. Rev. Ecol. Evol.* S. 39: 615–639.
- Litchman, E., M.D. Ohman and T. Kjørboe. 2013. Trait-based approaches to zooplankton communities. *J. Plankton Res.* 35: 473–484.
- Litchman, E., P. de Tezno Pinto, K.F. Edwards, C.A. Klausmeier, C.T. Kremer and M.K. Thomas. 2015. Global biogeochemical impacts of phytoplankton: a trait-based perspective. *J. Ecol.* 103: 1384–1396.
- Louette, G. and L. de Meester. 2005. High dispersal capacity of cladoceran zooplankton in newly founded communities. *Ecology* 86: 353–359.
- Lucas, C.H. 2000. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. In: J.E. Purcell, W.M. Graham and H.J. Dumont [eds.]. *Jellyfish Blooms: Ecological and Societal Importance*. Developments in Hydrobiology, Vol. 155. Springer, Dordrecht.
- Mackie, G.O. 1986. From aggregates to integrates: physiological aspects of modularity in colonial animals. *Phil. Trans. R. Soc. Lond. B* 313: 175–196.
- Madin, L.P. 1990. Aspects of jet propulsion in salps. *Can. J. Zool.* 68: 765–777.
- Mauchline, J. 1980. The biology of mysids and euphausiids. *Adv. Mar. Biol.* 18: 373–623.
- Mauchline, J. 1998. The biology of calanoid copepods. *Adv. Mar. Biol.* 33: 1–530.
- Mariash, H.L., M. Cusson and M. Rautio. 2016. Fall composition of storage lipids is associated with the overwintering strategy of *Daphnia*. *Lipids* 52: 83–91.
- McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples: a manual on methods for the assessment of secondary production in fresh waters. pp. 228–265. In: J.A. Downing and F.H. Rigler [eds.]. *A Manual on Methods for the Assessment of Secondary Production in Freshwaters*. Rigler, editors. IBP Handbook 17, Second edition. Blackwell Scientific Publications, Oxford, UK.
- McNaughton, S.J. 1977. Diversity and stability of ecological communities: A comment on the role of empiricism in ecology. *Am. Nat.* 111: 515–525.
- Merico, A., J. Bruggeman and K. Wirtz. 2009. A trait-based approach for downscaling complexity in plankton ecosystem models. *Ecol. Model.* 220: 3001–3010.
- Michels, J., J. Vogt and S.N. Gorb. 2012. Tools for crushing diatoms—opal teeth in copepods feature a rubber-like bearing composed of resilin. *Sci. Rep.* 2: 465.
- Michels, J. and S.N. Gorb. 2015. Mandibular gnathobases of marine planktonic copepods—feeding tools with complex micro- and nanoscale composite architectures. *Beilstein J. Nanotech.* 6: 674–685.
- Moody, E. and G. Wilkinson. 2019. Functional shifts in lake zooplankton communities with hypereutrophication. *Freshwater Biol.* 64: 608–616.

- Nielsen, J.M., E.L. Clare, B. Hayden, M.T. Brett and P. Kratina. 2017. Diet tracing in ecology: Method comparison and selection. *Methods Ecol. Evol.* 9: 278–291.
- Nock, C.A., R.J. Vogt and B.E. Beisner. 2016. *Functional Traits*. eLS. John Wiley & Sons, Ltd., Chichester. Doi: 10.1002/9780470015902.a0026282.
- Ohman, M.D., A.V. Drits, M.E. Clarke and S. Plourde. 1998. Differential dormancy of co-occurring copepods. *Deep-Sea Res. Pt II* 45: 1709–1740.
- Ohman, M.D. and J.B. Romagnan. 2016. Nonlinear effects of body size and optical attenuation on diel vertical migration by zooplankton. *Limnol. Oceanogr.* 61: 765–770.
- Paffenhöfer, G.A. and R.P. Harris. 1976. Feeding, growth and reproduction of the marine planktonic copepod *Pseudo-Calanus Elongatus Boeck*. *J. Mar. Biol. Ass. UK* 56: 327–344.
- Pangle, K.L. and S.D. Peacor. 2006. Behavioral response of *Daphnia mendotae* to the invasive predator *Bythotrephes longimanus* and consequent nonlethal effect on growth. *Freshwater Biol.* 51: 1070–1078.
- Patoine, A., B. Pinel-Alloul and E.E. Prepas. 2002. Influence of catchment deforestation by logging and natural forest fires on crustacean community size structure in lakes of the Eastern Boreal Canadian forest. *J. Plankton Res.* 24: 601–616.
- Petchey, O.L. and K.J. Gaston. 2002. Functional diversity (FD), species richness, and community composition. *Ecol. Lett.* 5: 402–411.
- Petchey, O.L. and K.J. Gaston. 2006. Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9: 741–758.
- Peters, R. 1983. *The Ecological Implications of Body Size*. Cambridge University Press, NY, USA.
- Pethybridge, H.R., C.A. Choy, J.J. Polovina and E.A. Fulton. 2018. Improving marine ecosystem models with biochemical tracers. *Annu. Rev. Mar. Sci.* 10: 199–228.
- Pierson, J.J., B.W. Frost and A.W. Leising. 2013. Foray foraging behavior: seasonally variable, food-driven migratory behavior in two calanoid copepod species. *Mar. Ecol. Prog. Ser.* 475: 49–64.
- Poff, N.L., J.D. Olden, N.K. Vieira, D.S. Finn, M.P. Simmons and B.C. Kondratieff. 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *J. N. Am. Benthol. Soc.* 25: 730–755.
- Pomerleau, C., A.R. Sastri and B.E. Beisner. 2015. Evaluation of functional trait diversity for marine zooplankton communities in the Northeast subarctic Pacific Ocean. *J. Plankton Res.* 37: 712–726.
- Razouls, C., F. deBovee, J. Kouwenberg and N. Desreumaux. 2005–2019. Diversity and Geographic Distribution of Marine Planktonic Copepods. URL: <http://copepodes.obs-banyuls.fr/>.
- Rizo, E.Z.C., Y. Gu, R.D.S. Papa, H.J. Dumont and B.-P. Han. 2017. Identifying functional groups and ecological roles of tropical and subtropical freshwater Cladocera in Asia. *Hydrobiologia* 799: 83–99.
- Reynolds, C.S. 1984. *The Ecology of Freshwater Phytoplankton*. Cambridge: Cambridge University Press.
- Reynolds, C.S., V. Huszar, C. Kruk, L. Naselli-Flores and S. Melo. 2002. Towards a functional classification of the freshwater phytoplankton. *J. Plankton Res.* 24: 417–428.
- Robson, B.J., G.B. Arhonditsis, M.E. Baird, J. Brebion, K.F. Edwards, L. Geoffroy et al. 2018. Towards evidence-based parameter values and priors for aquatic ecosystem modelling. *Environ. Modell. Softw.* 100: 74–81.
- Rosenfeld, J.S. 2002. Functional redundancy in ecology and conservation. *Oikos* 98: 156–162.
- Santoferrara, L.F. and G.B. McManus. 2021. Diversity and biogeography as revealed by morphologies and DNA sequences: Tintinnid ciliates as an example. pp. 85–118. *In*: M.A. Teodósio and A.B. Barbosa [eds.]. *Zooplankton Ecology*. CRC Press.
- Schleuter, D., M. Daufresne, F. Massol and C. Argillier. 2010. A user's guide to functional diversity indices. *Ecol. Monogr.* 80: 469–484.
- Schneider, T., G. Grosbois, W.F. Vincent and M. Rautio. 2017. Saving for the future: pre-winter uptake of algal lipids supports copepod egg production in spring. *Freshwater Biol.* 62: 1063–1072.
- Schmidt, K., A. Atkinson, K.J. Petzke, M. Voss and P.W. Pond. 2006. Protozoans as a food source for Antarctic krill, *Euphausia superba*: complementary insights from stomach content, fatty acids, and stable isotopes. *Limnol. Oceanogr.* 51: 2409–2427.
- Sodré, E.d.O. and R.L. Bozelli. 2019. How planktonic microcrustaceans respond to environment and affect ecosystem: a functional trait perspective. *Inter. J. Aquat. Res.* 11: 207–223.
- Steinberg, D.K. and M.R. Landry. 2017. Zooplankton and the ocean carbon cycle. *Annu. Rev. Mar. Sci.* 9: 413–44.
- Sterner, R.W. and J.J. Elser. 2002. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton.
- Strickler, J.R. 1982. Calanoid copepods, feeding currents, and the role of gravity. *Science* 218: 158–160.
- Tilman, D., J. Knops, D. Wedin, P. Reich, P. Ritchie and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300–1302.
- Thibaut, L.M. and S.R. Connolly. 2013. Understanding diversity-stability relationships: towards a unified model of portfolio effects. *Ecol. Lett.* 16: 140–150.

- Thuesen, E.V., F.E. Goetz and S.H.D. Haddock. 2010. Bioluminescent organs of two deep-sea arrow worms, *Eukrohnia fowleri* and *Caecosagitta macrocephala*, with further observations on bioluminescence in chaetognaths. *Biol. Bull.* 219: 100–111.
- Turner, J.T. and J.G. Ferrante. 1979. Zooplankton fecal pellets in aquatic ecosystems. *BioScience* 29: 670–677.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37: 130–137.
- Villar-Argaiz, M., J.M. Medina-Sanchez, L. Cruz-Pizarro and P. Carrillo. 2001. Inter- and intra-annual variability in the phytoplankton community of a high mountain lake: the influence of external (atmospheric) and internal (recycled) sources of P. *Freshwater Biol.* 46: 1017–1034.
- Villéger, S., N.W.H. Mason and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89: 2290–2301.
- Violle, C., M.L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel et al. 2007. Let the concept of trait be functional. *Oikos* 116: 882–892.
- Violle, C., P.B. Reich, S.W. Pacala, B.J. Enquist and J. Kattge. 2014. The emergence and promise of functional biogeography. *P. Natl. Acad. Sci. USA* 111: 13690–13696.
- Vogt, R.J., P.R. Peres-Neto and B.E. Beisner. 2013. Using functional traits to investigate the determinants of crustacean zooplankton community structure. *Oikos* 122: 1700–1709.
- Walker, B., A. Kinzig and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2: 95–113.
- Wallace, J.B. and J.R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. *Annu. Rev. Entol.* 41: 115–139.
- Weithoff, G. 2003. The concepts of ‘plant functional types’ and ‘functional diversity’ in lake phytoplankton—a new understanding of phytoplankton ecology? *Freshwater Biol.* 48: 1669–1675.
- Weithoff, G. and B.E. Beisner. 2019. Measures and approaches in trait-based phytoplankton community ecology—from freshwater to marine ecosystems. *Front. Mar. Sci.* 6: 40.
- Williamson, C.E., J.M. Fischer, S.M. Bollens, E.P. Overholt and J.K. Breckenridge. 2011. Toward a more comprehensive theory of zooplankton diel vertical migration: Integrating ultraviolet radiation and water transparency into the biotic paradigm. *Limnol. Oceanogr.* 56: 1603–1623.
- World Register of Marine Species Editorial Board. 2000–2019. URL: www.marinespecies.org.
- Yoshida, T., L.E. Jones, S.P. Ellner, G.F. Fussmann and N.G. Jr Hairston. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* 424: 303–306.